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Organic carbon mineralization in soils of a natural forest and a forest plantation of southeastern China



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ARTICLE INFO

Handling Editor: Junhong Bai

Keywords:
Incubation
Soil organic carbon
Temperature fluctuation
PLFAs
Microbial biomass carbon (MBC)
Subtropical forest

ABSTRACT

Understanding soil organic carbon (SOC) mineralization under different temperature regimes is critical for predicting SOC responses to climate change. Yet, the effects of altering temperature regimes on SOC mineralization remain poorly understood in forest plantations converted from natural forests. Forest conversion is extensive and could have major impact on SOC dynamics, so that this knowledge limits our ability of predicting the consequences of such land use change on carbon cycling. To fill this knowledge gap, we conducted a 360-day incubation experiment under constant and varying temperature regimes for soils of a natural forest and a Chinese fir (Cunninghamia lanceolata) plantation. Results showed that SOC mineralization was greater in the forest plantation soil than in the natural forest soil in both temperature treatments, possibly due to greater labile SOC in the forest plantation soil by 27-28%. The results suggested that replacing natural forests with forest plantations may increase CO2 emission via the mineralization of SOC. In the natural forest soil, SOC mineralization was greater in the varying temperature treatment relative to the constant temperature treatment but no difference was found in the forest plantation soil. Moreover, temperature sensitivity (Q10) of SOC mineralization was greater in the natural forest soil than the Chinese fir soil for the 0-180 day of the incubation. The difference in the response to the two temperature treatments between the two forest soils which was accompanied by difference in soil microbial communities. It was likely that soil microbes of the closed-canopy natural forest were less adapted to temperature fluctuations than soil microbes of the forest plantation soil as the canopy was rarely closed. Our results highlight that soil incubation experiments need to take temperature fluctuations into consideration to more accurately reflect SOC dynamics in the field, especially when evaluating the impacts of replacing natural forests with forest plantations on soil carbon dynamics.

1. Introduction

Soil is the largest terrestrial carbon sink storing 1576 Pg carbon (Eswaran et al., 1993). Forests contribute approximately 39% of global soil carbon stock (Janzen, 2004), therefore, small changes in forest soil carbon pool could have profound impacts on global carbon cycling (Schindlbacher et al., 2011; Ziegler et al., 2013). Soil organic carbon (SOC) mineralization is a major cause of soil carbon emission (Guillaume et al., 2015; Whitman and Lehmann, 2015). A large number of studies have examined patterns and controls of SOC mineralization across a variety of ecosystems (Fissore et al., 2008; Schütt et al., 2014;

Zhu and Cheng, 2011).

Mineralization of SOC is affected by many abiotic factors (e.g., temperature, moisture, soil properties, substrate availability) and biotic factors (e.g., soil microbial community structure and composition, vegetation types and enzyme activity) (Fissore et al., 2008; Hassan et al., 2014; Schütt et al., 2014; Stielstra et al., 2015). Among the factors affecting SOC mineralization, temperature has been the subject of many modeling (CENTURY model, ESMs model, DAYCENT model) and empirical studies of soil carbon dynamics (Parton et al., 1987; Lin and Zhang, 2012; Luo et al., 2016). Soil incubation has been widely used to evaluate the influences of warming on SOC mineralization but most soil

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incubation experiments were conducted under constant temperatures. Because the rate of SOC mineralization is sensitive to temperature, incubations conducted at constant temperatures may not accurately reflect patterns of SOC mineralization in the field.

A few incubation studies have involved varying temperature treatments but they were all performed by rotating between two fixed temperatures to mimic diurnal temperature fluctuations without taking seasonal fluctuations into consideration (Lomander et al., 1998; Zhu and Cheng, 2011; J.Y. Wang et al., 2014; Ci et al., 2015). Moreover, these studies provided inconsistent results on the magnitude and even the direction of the effect of varying temperature on SOC mineralization (Lomander et al., 1998; Zhu and Cheng, 2011; Ci et al., 2015). In a karst region of southwestern China, temperature fluctuations enhanced cumulative SOC mineralization in a limestone soil, but decreased it in a yellow soil after 56-day incubation (Ci et al., 2015). In contrast, a study in the Mediterranean region found that cumulative SOC mineralization was similar between constant temperature (20 °C) and varying temperature (15-25 °C) treatments in a farm soil and a grassland soil in California (Zhu and Cheng, 2011). The causes for these inconsistencies are not well understood but soil microbial communities may play an important role (Briones et al., 2014; Xu et al., 2018).

For example, it has been suggested that the dominant soil microbial populations at higher temperatures could metabolize substrates that are not used by microbial populations dominating at lower temperatures (Zogg et al., 1997). A reciprocal transplant study reported that soil microbial communities under oak canopies, were more sensitive to environmental change than those of open grasslands, which experienced greater temperature fluctuations (Waldrop and Firestone, 2006). The study also reported that microbial biomass, enzyme activities and microbial respiration decreased when microbial communities were transplanted from the oak forest to the grassland (Waldrop and Firestone, 2006). Temperature may also alter the composition of microbial communities that differ in SOC use efficiency (Six et al., 2006; Allison et al., 2010). For example, it has been reported that under higher temperatures, the assimilation efficiency of microbial communities tended to be smaller leading to greater soil carbon loss (Allison et al., 2010).

Because of the increasing timber demand, large areas of forests are experiencing high anthropogenic disturbances, leading to the conversion of approximately 4% of natural forests (11.8 million ha) to forest plantations globally between 1990 and 2015 (FAO, 2015). A large number of studies have examined the consequences of forest conversion on ecosystem services such as biodiversity, soil and water conservation and carbon sequestration (Pimentel et al., 1995; Guo and Gifford, 2002; Steffan-Dewenter et al., 2007; Yang et al., 2018). When natural forests are converted to forest plantations, soils are directly exposed to the external environments in the first several years so that diurnal temperature fluctuations could be substantial during the period. In oldgrowth Douglas-fir forests, diurnal soil temperature fluctuated 13.0–17 °C in the clear-cut but < 2.5 °C under the uncut forests (Chen et al., 1993). Yet, few studies have focused on the effect of forest conversion on soil carbon dynamics via the alternation of temperature regime.

In the current study, we investigated SOC mineralization in soils of a natural *Castanopsis kawakamii* forest and a planted Chinese fir plantation (*Cunninghamia lanceolata*) under two temperature regimes, a constant temperature regime and a varying temperature regime. We tested the following hypotheses. First, because many studies reported greater SOC mineralization in natural forests than in forest plantations (Chen et al., 2016; Yang et al., 2017), we hypothesized greater SOC mineralization in the natural forest soil than in the Chinese fir soil across the two temperature regimes (H_1). Second, soil microbial diversity generally decreases when a natural forest is converted to forest plantation (Yu et al., 2012; Vitali et al., 2016). The natural forest soil with a greater microbial diversity might be more adaptive to changes in environmental conditions including temperature fluctuations. Thus, we

hypothesized that SOC mineralization was different between the varying temperature regime and the constant temperature regime for the forest plantation soil but not for the natural forest soil (H_2). Third, because soil microbial communities are sensitive to temperature change, we hypothesized that microbial community composition was different between different temperature regimes across the two forests (H_3).

2. Materials and methods

2.1. Site description

Soil samples used for incubation were collected from the Nature Reserve of *C. kawakamii* (26°11′ N, 117°28′ E), in Fujian Province of southeastern China. The area has a typical subtropical monsoon climate, with mean annual air temperature of 19.6 °C and mean annual rainfall of 1665 mm, of which approximately 75% occurred from March to August between 1981 and 2010. The soil of the study site is classified as red soil (State soil Survey Service of China, 1998), equivalent to Ultisoils in the USDA Soil Taxonomy (Soil Survey Staff of USDA, 1999).

2.2. Soil sampling and preparation

Soil samples were collected from two forests, a ~200-yr *C. kawakamii* natural forest and a ~40-yr Chinese fir plantation. The dominant canopy trees of the natural forest were *C. kawakamii, Pinus massoniana, Cunninghamia lanceolata*, and *Schima superba*. The understory was dominated by shrubs of *Smilax china, Syzygium buxifolium, Litsea cubeba* and herbs of *Alpinia japonica, Rhizoma Cibotii*, and *Sarcandra glabra*. The Chinese fir plantation was converted from a natural *C. kawakamii* forest following clear-cutting in 1976. The understory of the Chinese fir plantation was dominated by shrubs of *Maesa japonica, Ficus hirta* and herbs of *Dryopteris sparsa, A. hayata*, and *Maesa forsk*. The soil texture is loamy clay in both forests. The natural forest soil had a carbon content of 29.4 g C kg $^{-1}$, nitrogen content of 1.8 g N kg $^{-1}$ and the Chinese fir plantation soil had a carbon content of 23.7 g C kg $^{-1}$ and nitrogen content of 1.8 g N kg $^{-1}$.

In each forest, three 20 m \times 20 m plots, separated at least 40 m from each other, were randomly selected. Soils of the top 0-10 cm were collected from five quadrats (1 m × 1 m) in each plot, one on each corner and one in the center in January 2014. Soil samples were taken in January because our varying temperature treatment of soil incubation began with January temperatures (see below). All soil samples from the three plots of the same forest were mixed to form a composite sample. Soil samples were brought to the laboratory in the field station immediately. Roots, litter, stones and other plant debris in each sample were removed, and then the sample was passed through a 2-mm sieve and homogenized. Three 10 g sieved soil samples of each forest were dried at 105 °C for determining gravimetric moisture content. Five soil samples of each forest were used for determining chemical and physical properties (pH), dissolved organic carbon (DOC), MBC, phospholipidderived fatty acids (PLFAs) prior to the incubation experiment. The remaining soil samples were stored at 4 °C for one week prior to the incubation experiment.

2.3. Experiment design

Soil samples were incubated under two temperature regimes for 360 days, a constant temperature regime at 20 °C (constant-T treatment), which was close to the annual mean temperature (19.6 °C) and same as the annual average temperature of the other temperature treatment, a varying temperature regime (varying-T treatment). To mimic the seasonal temperature fluctuation, the temperature set up in the varying-T treatment was based on the average daily maximum and minimum temperatures of each month measured in the field between January 2013 and December 2013 (Fig. 1). The incubation

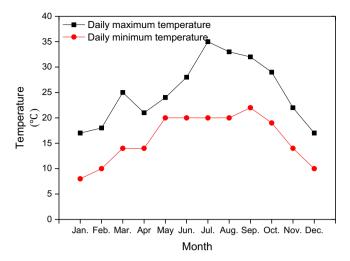


Fig. 1. The average daily maximum and minimum soil temperatures of each month based on temperatures of the 0–5 cm soil measured in the experimental site taken at a 5 min interval between January 2013 and December 2013.

temperatures were controlled by digital biochemical incubators (PRX-1000B, Ningbo Haishu Safe Instrument Experimental Factory, Ningbo, China). A total of 76 soil samples of each forest were used for the incubation experiment, 26 under the constant-T treatment and 50 under the varying-T treatment (detail see below).

Each soil sample (50 g dry) was placed in a 500 ml incubation jar. The soil moisture content was adjusted to 60% of field capacity prior to incubation. All samples were pre-incubated at 20 °C for two weeks to minimize the burst of respiration due to wetting the dry soils (i.e., Birch effect; Birch, 1958; Borken et al., 2003). The duration of two weeks for pre-incubation was chosen based on the study of Hamdi et al. (2011) which reported that SOC mineralization fluctuated considerably in the first two weeks but reduced afterwards. Deionized water was added to the soil twice a week to keep the loss of soil water within 2% (Chen et al., 2010). During the incubation, five samples of each temperature treatment were used for the determination of soil CO₂ evolution, In the constant-T treatment CO₂ evolution was measured at days 1, 3, 7, 14, 21, 30, 60, 90, 120, 150, 180, 270, and 360, and in the varying-T treatment it was measured at days 1, 3, 7, 14, 21, 30, 31, 33, 37, 44, 51, 60, 67, 74, 81, 90, 97, 104, 111, 120, 127, 134, 141, 150, 157, 164, 171, 180, 195, 210, 226, 240, 255, 270, 300, 330, and 360. The difference in sampling frequency was because the temporal patterns of soil CO2 evolution under varying-T treatment are less well understood than the pattern under constant-T treatment. Thus, we tripled the sampling frequency for the varying-T treatment compared to the constant-T treatment. In addition, unlike the constant-T treatment, in which the sampling was taken only once during the day, for each sampling day of the varying-T treatment, the sampling was conducted once during the day (i.e., under average daily maximum temperature) and once at the night (i.e., under average daily minimum temperature). During each measurement, compressed air was used to flush the headspace for 60 s to standardize the starting atmospheric CO2 concentration of each incubation jar (Whitaker et al., 2014a). After air washing, the incubation jar was taken to the original incubator immediately. Two hours later the headspace air (10 ml) was removed with a needle cylinder and stored in a gas sampling bag. The CO₂ content of gas samples was determined by gas chromatography (GC-2014, Shimadzu, Japan) within 24 h. The temperatures during the two-hour sampling were the same as the temperatures the samples were treated in the incubation. At the end of the incubation, DOC, MBC, PLFAs, SOC, soil organic nitrogen and pH were determined for each sample (i.e., five samples for each temperature treatment of each forest soil).

The DOC of each soil sample was extracted with deionized water

(5 g, soil: water ratio = 1:10) and filtered through a $0.45\,\mu m$ filter membrane. The extracted DOC was analyzed by using a total organic carbon (TOC) Analyzer (TOC-L CPH/CPN, Shimadzu, Kyoto, Japan). Microbial biomass carbon (MBC) was determined by a chloroform fumigation extraction method following Vance et al. (1987). For each incubation soil sample, two 5 g subsamples, one with and one without chloroform fumigation were extracted with 20 ml $0.5\,M$ K₂SO₄ (soil: extractant = 1:4) for 30 min and then filtered. The total organic carbon in the extracts was measured by a TOC Analyzer (TOC-L CPH/CPN, Shimadzu, Kyoto, Japan). MBC was calculated as:

$$MBC = E_C/K_{EC}$$

where E_C = (extractable C with fumigation - extractable C without fumigation) and K_{EC} = 0.45 (Hagerty et al., 2014).

In addition to the measurements at the beginning and end of the incubation experiment, during the incubation period, MBC was also determined at days 7, 30, 60, 90, 120, 180, and 270 for constant-T treatment at days 7, 30, 60, 74, 90, 104, 120, 134, 164, 180, 210, 240, 270, 300, and 330 for varying-T treatment, respectively. Similarly, the difference in sampling frequency was because the temporal patterns of MBC changes under varying-T treatment are not as well understood as the pattern under constant-T treatment. Thus, we increased the measurement frequency from 7 times for the constant-T treatment to 15 times for the varying-T treatment (i.e., 8 more times). The measurements of MBC during the incubation period was measured on three replicates at each measurement day. Unlike the measurements of soil CO₂ evolution, the three samples used in each MBC determination day could not be re-sued for future MBC determination, so that we had 24 more samples for varying-T treatment (45) than for constant-T treatment (21). The metabolic quotient (qCO₂) was estimated by dividing the mineralization rate by the corresponding MBC.

2.4. Microbial community structure

For each of the 5 incubation samples used for the determination of the above properties, a 10 g subsample was used for the determination of PLFAs. First, fatty acids were extracted and purified from each of the 10 g soil subsamples (stored at $-20\,^{\circ}$ C) and then analyzed following the procedures described by Wan et al. (2015). Total lipid abundance was calculated by summing the lipids with chain length ranging from 10 to 20 carbons. Gram-positive bacteria (GP) were represented by i14:0, i15:0, a15:0, i16:0, i17:0 and a17:0 (Zelles, 1999), gram-negative bacteria (GN) were represented by cy17:0, $16:1\omega$ 7c, $16:1\omega$ 9c, $18:1\omega$ 5c, $18:1\omega$ 7c and cy19:0 (Zelles, 1999), and fungi were represented by $18:1\omega$ 9 and $18:2\omega$ 6, 9 (Balser et al., 2005). The abundance of PLFAs was estimated by the amount of carbon and then converted to mole percentage PLFA-C. GP:GN and Fungi: bacteria (F:B) were, respectively, estimated as the ratio of sum of all GP to sum of all GN and the ratio of $(18:1\omega$ 9 + $18:2\omega$ 6, 9) to sum of all bacterial lipid.

2.5. Data analysis

2.5.1. SOC mineralization rate

Following Paré et al. (2006) SOC mineralization rate (r) was calculated as the change of CO_2 concentration in 2 h using the following equation:

$$r = 22.4 \times v/m \times \triangle c/\triangle t \times 273/(273 + T) * C_{M}$$
 (1)

where $\Delta c/\Delta t$ is the average CO_2 concentration difference per hour, ν is head space volume of incubation jar (total volume of jar minus soil volume), m is dry soil weight, T is the incubation temperature, and C_M is the molar mass of carbon (i.e., 12). The molar volume of CO_2 at the incubation temperature was determined using the ideal gas law.

The cumulative amount of soil organic carbon mineralized (C_m) was calculated using the following equation:

$$C_m = C_{m-1} + (R_p + R_{p-1})/2 * (D-D_{-1})$$
 (2)

where r is daily SOC mineralization rate, p is the incubation period, and D is the incubation day.

2.5.2. Temperature sensitivity

According to the exponential function, temperature sensitivity, Q_{10} or the increase of mineralization rate associated with a 10 °C increase in temperature, was estimated by Eqs. (3) and (4).

$$R = ae^{bT}, (3)$$

where R is SOC mineralization rate in μ g CO₂-C g⁻¹ h⁻¹, T is incubation temperature, a and b are fitting parameters, in which a is the SOC mineralization rate at 0 °C and b is the temperature dependence of SOC mineralization rate (Fierer et al., 2005).

$$Q_{10} = e^{10b}, (4)$$

The differences of microbial composition and soil properties between the forest plantation soil and natural forest soil were tested using one-way analysis of variance (ANOVA). Two-way ANOVA was used to test the effects of different soils and incubation times on Q_{10} values. The relationship between SOC mineralization and soil properties and microbial community composition was examined using Pearson correlations. All statistical analyses were performed using SPSS 19.0 (SPSS Inc., Chicago, IL, USA).

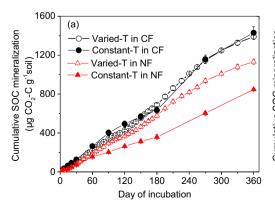
3. Results

3.1. Mineralization characteristics

After the 360-day incubation, cumulative mineralization amount was significantly greater in the forest plantation soil (1430 \pm 63 and 1390 \pm 27 μg CO $_2$ -C g^{-1} soil, for constant-T and varying-T treatment, respectively) than in the natural forest soil (848 \pm 12 and 1133 \pm 27 μg CO $_2$ -C g^{-1} soil, for constant-T and varying-T treatment, respectively) (both *P* values < 0.05). Cumulative SOC mineralization was not different between varying-T treatment (1390 \pm 27 μg CO $_2$ -C g^{-1} soil) and constant-T treatment (1430 \pm 63 μg CO $_2$ -C g^{-1} soil) in the Chinese fir soil (P=0.228, Fig. 2a). However, in the natural forest soil, the amount was greater in the varying-T treatment (1133 \pm 27 μg CO $_2$ -C g^{-1} soil) than in the constant-T treatment (848 \pm 12 μg CO $_2$ -C g^{-1} soil) (P<0.001, Fig. 2a). By the end of the incubation, approximately 5% of SOC was mineralized in the Chinese fir soil and 2.6–3.5% was mineralized in the natural forest soil (Fig. 2b).

3.2. Temperature sensitivity

There were no significant differences in Q_{10} between the natural forest soil (1.8 \pm 0.09) and the Chinese fir soil (1.7 \pm 0.03) for either the entire 360-day incubation or the 180–360 day of the incubation



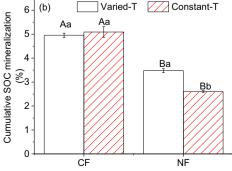


Fig. 3. The Q_{10} values of soil organic carbon mineralization of Chinese fir soil (CF) and natural forest soil (NF) in different incubation periods. Bars are standard deviation (n = 5). Different upper case letters indicate significant differences among different periods in soils of the same forest and different lower case letters indicate significant differences between soils of different forests at the same incubation period at $\alpha = 0.05$.

(Fig. 3). For the 0–180 day of incubation, however, it was greater in the natural forest soil than in the forest plantation soil (P = 0.048, Fig. 3). For both forest soils, Q_{10} was significant greater in the 180–360 day of incubation than that in the 0–180 day of incubation (both P values < 0.05) (Fig. 3).

3.3. Microbial metabolic quotient (qCO₂)

There was no significant difference of mean $q\text{CO}_2$ between the constant-T $(0.82\pm0.09\,\text{mg}\,\text{CO}_2\text{-C}\,\text{g}\text{C}_{\text{mic}}^{-1}\,\text{h}^{-1})$ and the varying-T $(0.75\pm0.10\,\text{mg}\,\text{CO}_2\text{-C}\,\text{g}\text{C}_{\text{mic}}^{-1}\,\text{h}^{-1})$ treatments for the forest plantation soil (Fig. 4a). However, for the natural forest soil it was significantly greater in the varying-T treatment $(2.13\pm0.26\,\text{mg}\,\text{CO}_2\text{-C}\,\text{g}\text{C}_{\text{mic}}^{-1}\,\text{h}^{-1})$ than in the constant-T treatment $(0.53\pm0.07\,\text{mg}\,\text{CO}_2\text{-C}\,\text{g}\text{C}_{\text{mic}}^{-1}\,\text{h}^{-1})$ (P<0.001, Fig. 4b). The temporal pattern of $q\text{CO}_2$ for the forest plantation soil was similar between varying-T and constant-T treatments but it was mostly smaller in the constant-T treatment than in the varying-T treatment for the natural forest soil (Fig. 4c and d).

3.4. Microbial community structure

Both soil type and temperature treatment had significant effects on total PLFAs (both P values < 0.05). The total extracted PLFAs decreased after the incubation in the forest plantation soil but increased in the natural forest soil in both temperature treatments (P < 0.05,

Fig. 2. The (a) temporal patterns of accumulative soil organic carbon (SOC) mineralization and (b) total soil organic carbon mineralized as a percentage of the original soil organic carbon in Chinese fir plantation soil (CF) and natural forest soil (NF) after 360-day incubation under (Constant-T) and varying temperature (Varying-T). Bars are standard deviation (n = 5). Different upper case letters indicate significant differences between CF and NF of the same temperature treatment and different lower case letters difference indicate significant differences between different temperature treatments of soils from the same forest at $\alpha = 0.05$.

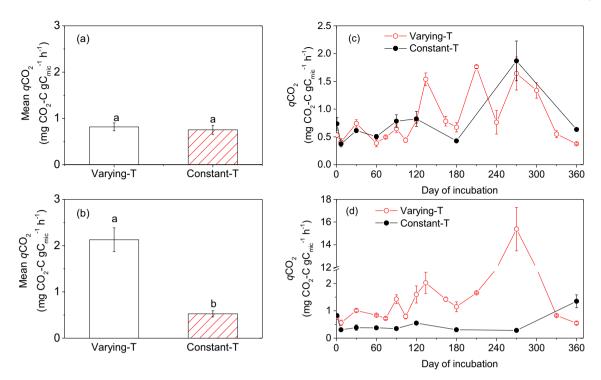


Fig. 4. The mean and temporal patterns of qCO $_2$ during incubation under constant temperature (Constant-T) and varying temperature (Varying-T) treatments in Chinese fir soil (CF, a, c) and natural forest soil (NF, b, d), respectively. Different lower case letters indicate significant differences at $\alpha = 0.05$.

Table 2). Between the two temperature treatments, the total PLFAs extracted were greater in constant-T treatment than in varying-T treatment for the natural forest soil but not the Chinese fir soil (Table 2).

The proportion of PLFAs attributable to bacteria, the largest among all microbe groups, decreased after the 360-day incubation in both temperature treatments in the Chinese fir soil (Table 2). However, in the natural forest soil it decreased in the constant-T treatment but increased in the varying-T treatment (Table 2). The proportion of PLFAs attributable to GP increased and that attributable to GN decreased after incubation in both forest soils (Table 2). In contrast, F:B increased in the forest plantation soil but decreased in the natural forest soil after incubation (Table 2). Between the two temperature treatments, F:B was smaller in the varying-T treatment than in the constant-T treatment in the forest plantation soil but it was not different between the two treatments in the natural forest soil (Table 2).

3.5. Soil properties and the relationship with SOC mineralization

Soil pH, DOC and MBC significantly decreased after the 360-day incubation for both the natural forest soil and the forest plantation soil (Table 2). Soil DOC in the varied-T treatment was greater than in the constant-T treatment for both forest soils (Tables1, 2). MBC in the varied-T treatment was greater than that in the constant-T treatment in the forest plantation soil but not in the natural forest soil (Tables1, 2). DOC and MBC were also greater in the Chinese fir soil than in the natural forest soil (Table 2). After the incubation soil DOC, MBC and pH, total PLFAs, GN, Fungi and F:B were all positively correlated with cumulative SOC mineralization, while GP:GN was negatively correlated with cumulative SOC mineralization across the two temperature regimes and the two forest soils (Table 3).

4. Discussion

4.1. SOC mineralization in natural and forest plantation soils

The greater SOC mineralization in the forest plantation soil than in

the natural forest soil (Fig. 2), which rejected our H_1 was unexpected because it contrasted with many previous studies that reported greater SOC mineralization in natural forests (Qi and Yang, 2017; Yang et al., 2017). Greater SOC mineralization in natural forests than forest plantations was often attributed to greater total SOC (Yang et al., 2017) or greater labile SOC, mainly DOC and MBC, in natural forests, which supported larger populations of soil microbes and through which thus enhanced SOC mineralization (J.Y. Wang et al., 2014; Chen et al., 2016). In our study, although total SOC was slightly smaller (19%) in the forest plantation, the amount of labile SOC, including DOC and MBC, was 27-28% grater in the forest plantation soil compared to the natural forest soil (Table 2). Thus, the overall greater SOC of the natural forest soil was mainly attributed to more recalcitrant SOC, which likely led to its smaller SOC mineralization. Because the Chinese fir plantation was converted from the adjacent natural forest, our result suggests that such forest conversion would lead to greater CO2 emission into the atmosphere via soil respiration.

The 5.1% SOC mineralization following the 360-day incubation in our study was considerably smaller than those reported by many studies in the temperate region. For example, along an altitudinal gradient in the temperate northern China, 5.1–14.1% of SOC was mineralized following 500-day incubation at 15 °C (Tian et al., 2016). In addition, a study of soil carbon responses to climate change in North Dakota and northern Texas reported 9.1–11.5% decreases of SOC following 336-day incubation at 25 °C and 35 °C (Conant et al., 2008). Low SOC mineralization (2–7%) has also been reported for several tropical and subtropical forests (Q.K. Wang et al., 2014; Wang et al., 2016). The greater SOC mineralization rates in the temperate region than the tropical and subtropical regions imply that there was likely proportionally more recalcitrant carbon in the tropical and subtropical region (Blum and Swaran, 2004; Lal, 2009).

4.2. Microbial respiration

The $q\text{CO}_2$ has been widely used as an indicator of the efficiency of microbial assimilation, with higher $q\text{CO}_2$ indicating lower assimilation rate and higher maintenance carbon demand (Anderson and Domsch,

Table 1 Soil properties and microbial community composition (mean \pm deviation) in Chinese fir soil and natural forest soil at the beginning of incubation (n = 5).

	Index	Chinese fir plantation	Natural forest
Soil properties	pH DOC (mg kg ⁻¹) MBC (mg kg ⁻¹)	3.98 ± 0.004 a 52.4 ± 2.1 a 244.6 ± 17.1 a	4.06 ± 0.004 b 41.7 ± 3.6 b 194.0 ± 11.2 b
Microbial community composition	Total PLFAs (nmol g ⁻¹ soil)	33.7 + 1.7 a	20.1 + 3.0 b
-	Bacteria (mol %)	44.9 ± 0.4 a	41.8 ± 0.5 b
	Fungi (mol%)	$4.3 \pm 0.1 a$	$5.3 \pm 0.1 \text{ b}$
	GP (mol%)	$27.2 \pm 0.3 a$	$21.6 \pm 0.8 b$
	GN (mol%)	$17.8 \pm 0.5 a$	$20.3 \pm 0.4 \mathrm{b}$
	F:B	$0.10 \pm 0.01 a$	$0.13 \pm 0.01 b$
	GP:GN	$1.5~\pm~0.1~a$	$1.1 \pm 0.1 \text{ b}$

Different lowercase letters indicate significant differences between Chinese fir soil and natural forest soil.

2010). The greater $q\mathrm{CO}_2$ in varying-T treatment relative to constant-T treatment in the forest plantation soil suggested that more SOC was consumed for maintenance respiration in the varying-T treatment and this would reduce microbial carbon use efficiency. According to the metabolic theory (Brown et al., 2004), if microbes are active for a long period, cumulative maintenance respiration would be large but the population size of microbes would be small. This could explain the greater $q\mathrm{CO}_2$ but smaller MBC in the natural forest soil relative to the Chinese fir soil. This suggests that upon conversion of natural forests to forest plantations, less carbon will be allocated to soil microorganisms, and more soil carbon would be emitted through microbial respiration. This result also echoes the greater response of the natural forest soil to varying-T treatment, which would result in greater SOC mineralization in the natural forest soil compared to the forest plantation soil.

4.3. Temperature sensitivity

The greater SOC mineralization in the varying-T treatment than the constant-T treatment in the natural forest soil but not in the Chinese fir soil is contradictory to the prediction of H_2 and probably reflected the differences in temperature sensitivity between the two forest soils. Temperature sensitivity is often used to describe thermal response of SOC mineralization (Kirschbaum, 2006; Vanhala et al., 2008; Bai et al., 2017). The greater Q_{10} of SOC mineralization in the natural forest soil during the first 180 days indicates its greater temperature sensitivity compared to the Chinese fir soil.

The difference in temperature sensitivity between the natural forest

soil and the Chinese fir soil may be related to differences in temperature fluctuations between the two forests. Both diurnal and seasonal soil temperature fluctuations were substantial in the forest plantation during the first several years following forest conversion, when the trees were small and the forest canopy was very open. Even in later stages, the Chinese fir plantation rarely reached the close-canopy state due to mechanical thinning, which was practiced to minimize competition for light and enhance the growth of trees for harvest. The Chinese fir plantation was thinned in 1987 and the canopy was not closed when we conducted the study. In contrast, the 200-yr natural forest had a very complete canopy cover so that soil temperature fluctuations should be substantially smaller relative to that in the forest plantation. Thus, compared to soil microbes in the forest plantation, soil microbes in the natural forest had experienced smaller temperature fluctuations and as such were more sensitive (less adaptive) to temperature fluctuations. The greater temperature sensitivity of the natural forest soil likely contributed to its greater responses (increases) of SOC mineralization to varying-T treatment.

Temperature sensitivity of SOC mineralization also varied through time as indicated by the greater Q_{10} in the 180–360 day of incubation than in the 0-180 day of incubation (Fig. 3). The temporal variation can be explained by the "carbon-quality-temperature" theory (Bosatta and Ågren, 1999). According to the theory, the decomposition rate of labile substrates (e.g., DOC) has weaker temperature dependence than that of low quality substrates (Bosatta and Ågren, 1999). Many studies also suggested that soil CO₂ emission was mainly from DOC in the early stages of incubation (Conant et al., 2008; Gershenson et al., 2009). Through the mineralization process, labile substrates were progressively mineralized leaving greater proportions of more recalcitrant substrates in the SOC leading to the greater Q₁₀ in the later than early stages of soil incubation (Fig. 3). Because more recalcitrant SOC has greater temperature sensitivity (Conant et al., 2008, 2011), warming may have greater impacts on soil carbon dynamics in the tropical and subtropical region than in the temperate region.

4.4. Shifts of soil microbial community composition

Mineralization of SOC is mediated by soil microorganisms, mainly bacteria and fungi (Schmidt et al., 2011). In our study, soil microbial community composition shifted after incubation (Tables 1, 2). In the incubation experiment, only deionized water and no exogenous SOC was added so that substrate availability gradually decreased. Among the different groups of bacteria, GN is more effective in decomposing fresh plant detritus, whereas GP is more effective in decomposing SOM (Potthoff et al., 2005; Kramer and Gleixner, 2006). Therefore, GP increased, GN decreased and the ratio of GP:GN increased following the

Table 2
The changes (after incubation – before incubation) in cumulative SOC mineralization, DOC, MBC, pH, C:N, total PLFAs, bacteria, fungi, GP, GN, F:B and GP:GN (mean \pm deviation) in Chinese fir soil and natural forest soil in constant temperature (Constant-T) and varying temperature (Varing-T) treatments (n = 5).

	Chinese fir plantation		Natural forest	
	Constant-T	Varying-T	Constant-T	Varying-T
DOC (mg kg ⁻¹)	−15.6 ± 1.4 Aa	−10.0 ± 1.8 Ab	−13.7 ± 3.0 Aa	−11.0 ± 3.2 Aa
MBC (mg kg $^{-1}$)	$-77.6 \pm 5.5 \text{ Aa}$	$-45.9 \pm 6.1 \text{ Ab}$	$-44.7 \pm 19 \text{ Ba}$	$-57.5 \pm 5.1 \text{ Ba}$
pH	$-0.30 \pm 0.01 \text{ Aa}$	$-0.26 \pm 0.04 \text{ Ab}$	$-0.46 \pm 0.02 \text{ Ba}$	$-0.41 \pm 0.01 \text{ Bb}$
C:N	$1.1 \pm 0.6 \text{Aa}$	$0.7 \pm 0.5 \text{ Aa}$	$-1.2 \pm 0.4 \mathrm{Ba}$	$-1.4 \pm 0.4 \mathrm{Ba}$
Total PLFAs (nmol g ⁻¹ soil)	$-6.2 \pm 4.2 \text{ Aa}$	$-3.2 \pm 3.6 \text{ Aa}$	$35.6 \pm 8.1 \text{ Ba}$	$9.9 \pm 5.2 \text{ Bb}$
Bacteria (mol%)	$-4.2 \pm 0.4 \text{ Aa}$	$-2.3 \pm 1.5 \text{ Ab}$	$-1.3 \pm 0.5 \mathrm{Ba}$	$2.9 \pm 1.0 \text{ Bb}$
Fungi (mol%)	$0.8 \pm 0.2 \text{Aa}$	$0.8 \pm 0.1 \text{ Aa}$	- 1.4 ± 0.2 Ba	$-1.5 \pm 0.2 \text{ Bb}$
GP (mol%)	$1.0 \pm 0.2 \text{Aa}$	$1.64 \pm 0.9 \text{ Aa}$	$7.46 \pm 1.1 \text{ Ba}$	$10.4 \pm 0.9 \text{ Bb}$
GN (mol%)	$-5.3 \pm 0.3 \text{ Aa}$	$-3.9 \pm 0.9 \text{ Ab}$	$-8.7 \pm 0.7 \text{ Ba}$	$-7.5 \pm 0.3 \text{ Bb}$
F:B	$0.03 \pm 0.003 \text{ Aa}$	$0.02 \pm 0.004 \text{ Aa}$	$-0.03 \pm 0.007 \mathrm{Ba}$	$-0.04 \pm 0.005 \text{ Bb}$
GP:GN	$0.7 \pm 0.1 \text{Aa}$	$0.6 \pm 0.1 \; \text{Aa}$	$1.5 \pm 0.2 \text{ Ba}$	$1.4 \pm 0.1 \; \text{Ba}$

Different lowercase letters indicate significant differences among the treatments in the same forest, and different uppercase letters indicate significant differences between Chinese fir soil and natural forest soil.

Table 3The relationship between cumulative carbon mineralization and soil properties.

	SOC mineralization		
	r	P value	
Total PLFAs	-0.831**	< 0.001	
GP	-0.309	0.184	
GN	0.584**	0.007	
Fungi	0.848**	< 0.001	
Bacteria	0.096	0.689	
DOC	0.876**	< 0.001	
MBC	0.537*	0.032	
pH	0.833**	< 0.001	
GP:GN	-0.710**	< 0.001	
F:B	0.744**	< 0.001	

^{*} and ** indicate significant correlations at P < 0.05 and P < 0.01, respectively.

P-values in bold indicate a statistically significant difference.

incubation in both constant- and varying-T treatments. Due to the close relationship between soil microbial community and SOC mineralization (Koranda et al., 2013; Tang et al., 2018; Whitaker et al., 2014b), the difference in the composition of soil microbial communities between the two temperature treatments was likely the result of their difference of SOC mineralization.

Interestingly, although many studies reported a positive relationship between MBC and PLFAs (Bailey et al., 2002; Leckie et al., 2004), we did not find such a relationship possibly due to the very low soil pH in our study. It has been shown that when soil pH falls below 5.0, soil microbes may experience aluminum toxicity resulting in significant shifts of microbial community structure (Pietri and Brookes, 2008). The pH of soils in our studied forests was approximately 4.0 (Table 1). Thus, the high soil acidity probably led to major shifts in microbial community structure and, therefore, the deviation from the positive relationship between MBC and PLFAs.

5. Conclusions

In contrast to the widely reported greater SOC mineralization in natural forests than forest plantations, we found greater SOC mineralization in the forest plantation soil than in the natural forest soil, probably due to their small difference of SOC and the greater proportion of labile carbon in the forest plantation soil. We also found that varying-T treatment accelerated CO2 emission in the natural forest soil but not in the forest plantation soil and the Q_{10} of SOC mineralization was greater in the natural forest soil during the first 0-180 day, possibly because the soils of the two forests had experienced different temperature regimes prior to the incubation. Soils under the close-canopy natural forest rarely experienced the applied temperature fluctuations, whereas the forest plantation soil was exposed to greater temperature fluctuations because the forest canopy rarely closed. We also found greater qCO₂ but smaller MBC in the natural forest soil relative to the Chinese fir soil, suggesting that when natural forests are converted to forest plantations, less carbon will be allocated to the soil microorganisms, and more CO₂ will be emitted through microbial respiration. Our results highlight that given the large scale conversion of natural forests to forest plantations that is taking place in China and many other tropical and subtropical forests (FAO, 2015), the consequences of such conversion on CO₂ emission deserve further investigations.

Acknowledgements

This study was supported by the National Natural Science Foundation of China (grand number U1505233), the Strait Postdoctoral Exchange Program of China, and the National Key Basic Research Program of China (grant number 2014CB954003). We sincerely thank

Wei Li, Benjia Zhao, Xi Qiu for their help in the field work and laboratory analyses. We also thank Dr. Craig Martin for his help in proofread the revised manuscript.

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